Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination

Sophie Schwartz*†‡, Pierre Maquet§, and Chris Frith¶

*Institute of Cognitive Neuroscience, 17 Queen Square, London WC1N 3AR, United Kingdom; †Neurology and Imaging of Cognition, University Medical Center, 1 Michel-Servet, 1211 Geneva, Switzerland; §Cyclotron Research Centre (B30), University of Liège, 4000 Liège, Belgium; and ¶Wellcome Department of Imaging Neuroscience, 12 Queen Square, London WC1N 3BG, United Kingdom

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Visual texture discrimination has been shown to induce long-lasting behavioral improvement restricted to the trained eye and trained location in visual field [Karni, A. & Sagi, D. (1991) *Proc. Natl. Acad. Sci. USA* 88, 4966–4970]. We tested the hypothesis that such learning involves durable neural modifications at the earliest cortical stages of the visual system, where eye specificity, orientation, and location information are mapped with highest resolution. Using functional magnetic resonance imaging in humans, we measured neural activity 24 h after a single session of intensive monocular training on visual texture discrimination, performed in one visual quadrant. Within-subject comparisons between trained and untrained eye for targets presented within the same quadrant revealed higher activity in a corresponding retinotopic area of visual cortex. Functional connectivity analysis showed that these learning-dependent changes were not associated with an increased engagement of other brain areas remote from early visual cortex. We suggest that these new data are consistent with recent proposals that the cellular mechanisms underlying this type of perceptual learning may involve changes in local connections within primary visual cortex. Our findings provide a direct demonstration of learning-dependent reorganization at early processing stages in the visual cortex of adult humans.

Neural plasticity involves lasting modifications of the structure and function of the brain in response to environmental changes. During perceptual learning, the ability to discriminate differences in the attributes of simple stimuli progressively improves with practice. For basic feature-discrimination learning, recordings of cells in adult monkeys have recently shown that cortical plasticity underlying the behavioral improvement may occur as early as in primary cortex (for a review, see ref. 1). Such plastic changes could permit durable improvements in performance with practice while maintaining a great potential for flexible processing of sensory information.

In the visual domain, psychophysical findings indicate that improvement in texture discrimination task (TDT) is often restricted to the visual features that have been trained, such as a particular location in the visual field, the spatial configuration of the stimulus elements, or monocular exposure (2, 3). Such specificity for elementary features in TDT learning might reflect experience-dependent changes taking place at early processing stages in the visual system, at the level where monocularity and retinotopic organization of the visual inputs are still retained, and where different orientations are processed separately (4). In non-human primates, electrophysiological studies of visual learning have implicated an increase in neuronal sensitivity in primary visual cortex (V1) that is specific for relevant stimulus attributes (e.g., location, orientation) (5), as well as a modulation of neuronal responses by contextual influences via intrinsic long-range horizontal connections (6, 7). Thus, both cellular and behavioral evidence suggest that TDT learning may primarily rely on local changes at early cortical stages in visual processing.

However, such experience-dependent neural changes may also involve a larger network of brain regions, including feedback influences coming from higher-order cortical areas (8, 9). For example, perceptual learning requires the active, attentive participation of the observer, as shown by the lack of behavioral improvement after passive stimulation (6, 10). Subsequent improvement in performance after learning might therefore result from more effective attention, engaging a distributed network of brain regions (11). Moreover, higher-level areas in extrastriate cortex (e.g., V4) have also been implicated in certain TDT in monkeys (12, 13).

Here, we designed a functional MRI (fMRI) experiment to determine the neural substrates that mediate visual perceptual learning in humans. We used a well documented TDT paradigm thought to induce neural modifications at the earliest cortical stages where eye specificity, orientation, and location information are mapped with highest resolution (3, 14, 15). In this task, participants are asked to determine the orientation of a peripheral target texture while simultaneously monitoring the identity of a central letter (Fig. 1*A*). Performance is known to improve only for the trained retinal location and the trained eye (3, 16). Improvement in TDT is seen only after the first night of sleep (14, 15, 17) or after a restorative nap (18), and performance may continue to increase over the next 4 days after a single session, without additional intervening training (14). Eye-specific effects found in this task have not been replicated when using slightly different methodologies (e.g., ref. 19). However, the effectiveness of learning after a single session (14) might potentially conceal the monocular selectivity of learning with the trained eye when the untrained eye has also been initially exposed to the task at baseline (19). Also, retinotopy and monocularity are specific characteristics of the task used here and not present in other visual learning paradigms like pop-out detection (20).

We obtained whole-brain fMRI scanning 1 day after intensive practice with the task. By training one eye for targets presented always in the same visual quadrant, we could directly contrast brain activity associated with performing the task with either the trained or the untrained eye. All visual targets fell onto the same retinotopic regions of visual cortex and varied only as a function of the learning status of the tested eye (i.e., trained or untrained). Because both trained and untrained targets were shown at the same location in the visual field (but to different eyes), we were able to test whether any learning-dependent changes in blood oxygenation level-dependent (BOLD) response would occur 24 h after practice within early visual cortex corresponding to the tested visual quadrant. By using whole-brain imaging and functional connectivity analysis, we also examined whether changes in visual cortex were associated with concomitant changes in other brain areas.

Methods

Participants. Sixteen right-handed healthy volunteers (three males; age range 20–33 years; mean age 26 years) gave informed

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Abbreviations: TDT, texture discrimination task; fMRI, functional MRI; BOLD, blood oxygenation level-dependent; SOA, stimulus-to-mask onset asynchrony; SPM, statistical parametric map.

See commentary on page 16519.

‡To whom correspondence should be addressed. E-mail: s.schwartz@ucl.ac.uk.

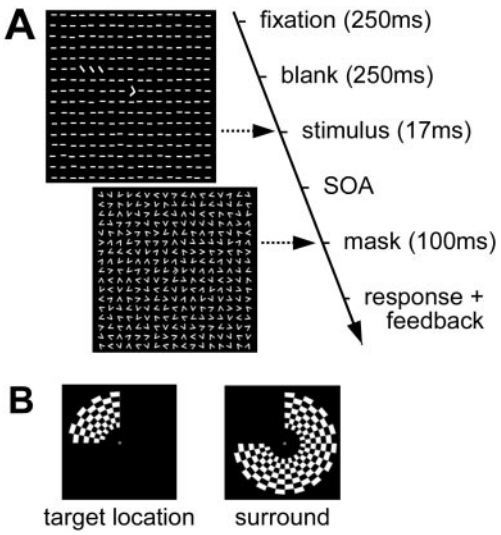

Fig. 1. (*A*) Sequence of successive displays in a single trial of the TDT. For each trial, participants had to identify a central letter and the orientation of a target texture. Immediate auditory feedback was provided for the letter identification. SOA was progressively decreased from 460 to 80 ms during training, but then was kept constant at 200 ms during scanning. (*B*) Flickering checkerboard stimuli used in the retinotopic localizer protocol, with stimulation of the upper left quadrant used for the experimental task, alternating with stimulation of the other three quadrants.

consent to participate in a study approved by the Joint National Hospital for Neurology and Neurosurgery/Institute of Neurology Ethics Committee. All subjects were free from psychiatric or neurological history. None of them was on medication. Fourteen participants had normal vision, and two had corrected-to-normal vision (contact lenses).

Behavioral Task. The TDT was designed as previously described (3). An intensive training session was given 24 h before scanning, during which participants performed the task using only one eye (eight right and eight left, random allocation across participants). The task was otherwise identical during training and fMRI scanning. On each trial, participants had to identify a central letter (randomly rotated L or T) and the orientation of a peripheral target texture (Fig. 1*A*). In this paradigm, the central task ensures good fixation and shows only modest improvement with practice (3), whereas the detection of the peripheral target texture represents the learning-dependent component of the task, with improved discrimination of orientation after practice. Each peripheral target was made of three contiguous diagonally oriented bars (horizontal or vertical configuration) appearing at various positions in the upper left quadrant (2.5–5° from center) on a background of 17 × 17 slightly jittered horizontal bars (0.43 × 0.07° each, spaced 0.76° apart). Both training and scanning settings were matched as closely as possible. An opaque divider was placed between each participant's face and the center of the screen, allowing for monocular presentations. The display size was 13 × 13° of visual angle, on either side of the screen (2.8° gap). Both training and scanning were performed in a dark environment, with restricted head movements, by using a 1,024 × 768 pixel screen resolution, 60 Hz refresh rate, and a MATLAB Toolbox (www.mathworks.com/) for presenting stimuli and recording responses with precise timing (COGENT 2000, www.fil.ion.ucl.ac.uk/cogent2000.html). The stimuli were always shown in the upper left part of the visual field, thus projecting in the lower part of the right visual cortex regardless of whether they were seen by the left or right eye. Axons from the temporal retina cross in the optic chiasm and project to ocular dominance columns in the contralateral hemisphere, whereas axons from the nasal retina do not cross and project to ocular dominance columns in the ipsilateral hemisphere (21).

Monocular training was performed during a single session 24 h before scanning. A total of 1,760 training trials were presented in two successive identical parts comprising 22 blocks (40 trials each) with decreasing time intervals between target display and mask [stimulus-to-mask onset asynchrony (SOA)]: one block each at 460, 360, 260, and 220 ms, followed by three blocks each at 180, 160, 140, 120, 100, and 80 ms. An immediate auditory feedback was provided for the letter identification. No feedback was given for the target-texture discrimination. SOAs provided a critical independent variable assessing the degree of learning, inversely related to task difficulty. The threshold SOA (≥80% correct responses) for the group stabilized at 200 ms during the second series of blocks. Note that monocular training is highly demanding, leading to poorer average performance than binocular presentations (20).

The fMRI session involved the same task but now performed with the trained and untrained eyes in an alternating sequence. A single continuous run of scanning (20 min) consisted of a succession of four different conditions, starting by a fixation block followed by a task block of six discrimination trials presented to one eye (each block ≈18 s), immediately followed by a fixation block and a task block presented to the other eye, and so on for 12 times. Visual targets were always presented within the upper-left quadrant, for both the "learned" and "new" conditions (i.e., trained and untrained eyes, respectively). SOAs were fixed at 200 ms for both eyes in all participants, based on pilot experiments showing reliable group performance with such values irrespective of training. Performance during scanning was measured by the total percent of correct responses.

Because the main goal of the experiment was to compare the activity of the same cortical area, mapping the same location in the visual field but using different eyes (trained or untrained), we performed two additional retinotopic localizer sequences after the main scan to identify voxels specifically responding to the tested visual quadrant. These sequences were performed separately for each eye and consisted in a succession of blocks with flickering checkerboards presented to the upper left quadrant versus the other three quadrants (Fig. 1*B*) while participants maintained central fixation.

MR Data Collection. A 2T Siemens VISION system (Siemens, Erlangen, Germany) provided high-resolution T1 anatomical volume images (matrix, 256 × 176 × 256; voxel size: 1 × 1 × 1.5 mm^3) and T2*-weighted functional transverse slices (TE = 40 ms; TR = 3.2 s; matrix size 64 × 64 × 42; voxel size: 3 × 3 × 3 mm^3) with BOLD contrast. Visual stimuli were projected onto a specially designed nonmagnetic projection screen (covering 28.8 × 20.6° of visual angle), equipped with a divider placed between the participant's eye and a mirror reflecting the screen. Participants viewed monocularly each side of the screen located 30 cm from their eyes via the mirror.

Three separate successive functional scanning sessions were acquired by using block designs with identical epoch duration (18.24 s). The first six volumes of each scanning session were discarded to allow for magnetic saturation effect. In the main experimental session testing for perceptual learning effects (286 volumes), epochs of monocular fixation followed by epochs of active monocular discrimination (six trials each) alternated for the trained and nontrained eye. Condition order was counterbalanced across participants. In the subsequent retinotopic localizer protocols (64 volumes for each eye), flickering checkerboard patterns were presented during epochs of 18.24 s in the upper left quadrant, between 2.5 and 5° of visual angle away from the center, corresponding to the average location of target-

texture stimuli in the main experimental task, and alternated with epochs of flickering checkerboards in the remaining three quadrants (Fig. 1).

fMRI Data Analysis. Statistical parametric mapping software (SPM99, www.fil.ion.ucl.ac.uk/spm/spm99.html) was used for image processing and analysis. Functional volumes from the main test and localizer sessions were corrected for head motion, corrected for slice acquisition times, spatially normalized to an EPI template of $3 \times 3 \times 3$-mm^3 voxels conforming to the Talairach space, and smoothed with a Gaussian kernel of 8-mm full-width at half-maximum. High-pass filtering (1/140 Hz) removed participant-specific drifts in signal. For the main test and localizer sessions, the mean activity evoked in the conditions of interest were modeled by boxcar waveforms convolved with a canonical hemodynamic response function and then used as regressors in a multiple regression analysis. Movement parameters were added as covariates of no interest. The experimental test session also included baseline monocular fixation epochs as covariates of no interest, controlling for task-unspecific monocular effects.

The time series for each voxel was best fitted (least-squares fit) by using a linear combination of the regressors, resulting in a statistical parametric map of the t and Z values for the comparison of interest, corrected for volume of interest (F map for all modeled effects) and for multiple comparisons. Differences in regional BOLD signal for the contrasts of interest were identified by the height and location of their peak. We performed a second-level analysis, corresponding to a random effects model, to account for individual anatomical differences in visual cortex and for intersubject variance in the main effect of learning. Parameter estimates were extracted for each participant at the peak of the occipital cluster showing learned > new increases that were comprised within the area of visual cortex activated by the retinotopic localizer in this individual and closest to the group peak. Activity for the learned and new conditions in these voxels was compared in a one-sample t test across all individual participants.

Changes in Functional Connectivity. To examine whether the pattern of correlations between the right visual cortex and other distant areas was modulated by the training condition, a psychophysiological interaction analysis was performed (22). A new linear model was designed using three regressors (plus covariates of no interest as in the initial model above). One regressor was the difference between the two main regressors of interest (learned minus new blocks of stimulation). The second regressor was the activity in the right medial occipital cortex at the peak of the learning-related effect ($x, y, z = 15, -81, -3$; Fig. 2*A*). The third regressor representing the psychophysiological interaction of interest was the multiplication of the first and second regressors. Significant fit for this new regressor indicated a learning-specific change in the contribution of any reported area to the activity in the right medial occipital cortex (voxelwise threshold, $P < 0.001$, uncorrected; cluster size threshold, $P < 0.05$) (22). Significant coupling was considered for those areas whose activity showed significant positive regression slopes ($P < 0.001$) with the activity in the visual cortex during either the new or the trained condition.

Results

Behavioral Data. Behavioral performance during scanning confirmed that intensive practice on the TDT was effective 24 h later. Percentages of correct responses for peripheral target-texture discrimination was higher with the trained eye as compared with the untrained eye [(%) M = 57.75, M = 53.06; t (15) = 3.34, $P < 0.005$, respectively], confirming the monocular specificity of the task. There was only a small trend for the central letter identification to improve on the trained eye [(%) M = 72.88, M = 70.56; t (15) = 1.73, $P = 0.052$, respectively], as previously observed (3), indicating that participants were fixating equally well during the learned and new conditions.

An apparent decrease in absolute performance between training and scanning is probably due to special characteristics of the scanning environment (i.e., supine position, noise, stress, switching between eyes, etc.) that could affect such a difficult task despite our careful matching of the visual stimulus parameters (visual angle and contrast, display resolution and refresh rate, etc.). Performance was much better during a postscanning control experiment performed in a silent and less stressful environment with nonswitching presentations. Nine subjects were tested immediately after the fMRI acquisition, while still lying in the scanner, and thus presented with exactly the same stimulus display as during fMRI scanning. Each eye was tested for 48 trials presented in one sequence to the upper left (as trained) and 48 trials in one sequence to the lower right (untrained) quadrants (24 trials at short SOAs, 120–140 ms, and 24 trials at longer SOAs, 160–180 ms). Despite SOAs being shorter than during fMRI (% correct at 120–140 ms, trained eye = 73.89; untrained eye = 64.44), the decline in performance with shorter SOAs was greater for the untrained eye-trained quadrant than for the trained eye-trained quadrant, where performance remained high even at short SOAs [t (16) = 2.01, $P < 0.05$]. Performance on the new quadrant also showed relatively low performance at short SOAs for both the trained and untrained eye [(%) M = 53.89, M = 59.44, respectively]. This pattern of data provides further evidence for learning effects specific to the trained eye and trained quadrant.

Neuroimaging. Group analysis of the fMRI scans from the 16 participants revealed a single cluster of significant activation in the lower bank of the right calcarine sulcus (Fig. 2) when comparing discrimination in the learned condition (trained eye) relative to the new condition (untrained eye). The maximum of visual activation was found at coordinates $x, y, z = 15, -81, -3$ mm (cluster size = 88 voxels; Z value = 4.6; $P < 0.01$ corrected). All of the voxels more activated in the learned condition were included in the retinotopically activated region that was separately identified by the localizer procedure (Fig. 2*B*). No other significant effect was observed throughout the brain for the same contrast (new > learned), even at more liberal threshold ($P \leq 0.001$ uncorrected).

Single-subject analyses confirmed these results. Parameter estimates of activity at the right occipital peak extracted from each individual dataset showed highly significant increases when comparing responses to targets presented to the trained versus untrained eye [t (15) = 5.9, $P < 0.001$] (Fig. 2*C*). Representative individual statistical parametric maps (SPMs) are shown in Fig. 2*E*. Activation foci observed on individual SPMs were compatible with an increase peaking in V1, whereas an activation in other retinotopic areas (e.g., V2) would be more ventral for such upper field targets (23, 24). Furthermore, only V1 is known to contain neurons with monocular-dominant responses as found here (21), whereas neurons in subsequent cortical visual areas (V2 and beyond) exhibit similar responses to inputs from both eyes (25). Taken together, these results suggest that regional brain changes associated with learning to discriminate a parafoveal target texture occurred in early visual areas, in a region of the occipital cortex not only corresponding to the retinotopic target-texture location but also maintaining monocular specificity.

We also examined the reverse comparison (new > learned condition), but this showed only a small cluster of activation (8 voxels) in the right supramarginal gyrus that did not survive statistical correction for multiple comparisons ($x, y, z = 51, -42, 21$; Z value = 3.75; $P = 0.226$ corrected).

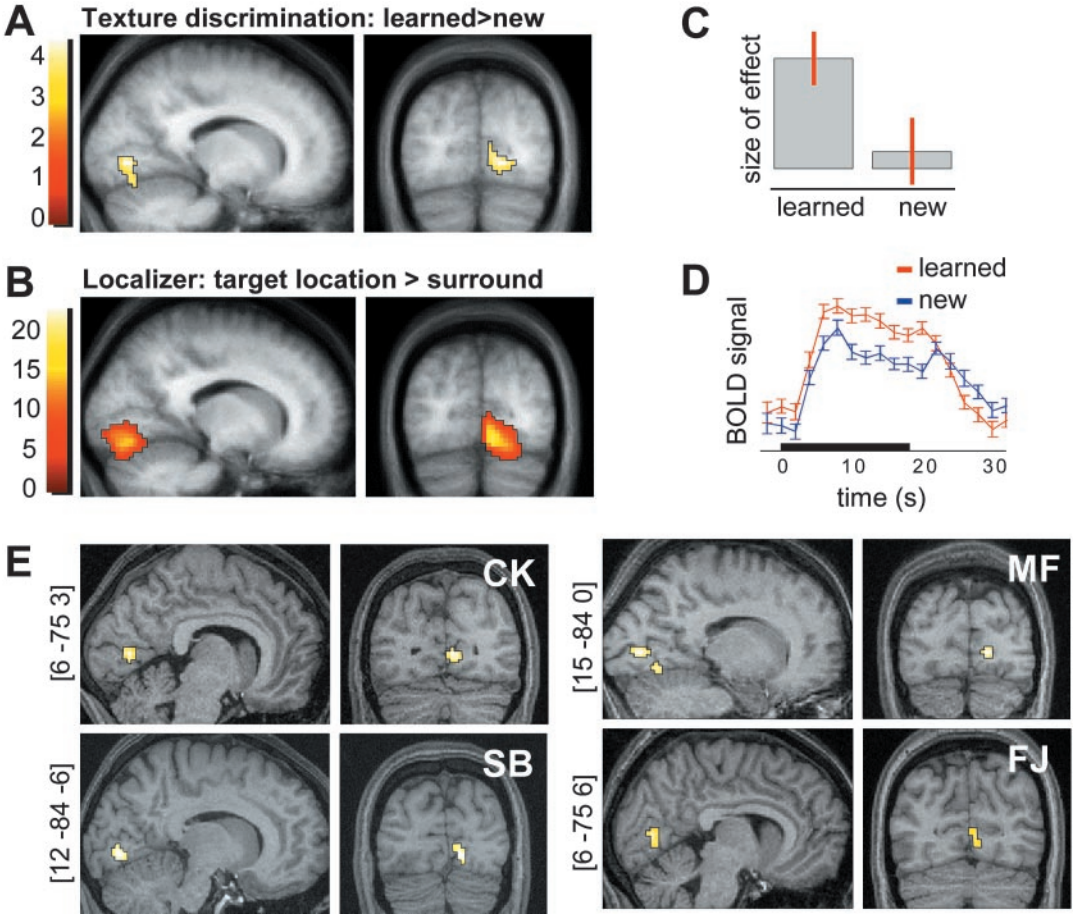

Fig. 2. Main effect of learning on fMRI activity. (*A*) Increased signal in the lower bank of the right calcarine sulcus (right lingual gyrus) in the learned condition (trained eye) as compared with the new condition (untrained eye). Group results are shown superimposed on the mean structural T1-weighted MRI of the 16 participants (coregistered to the functional acquisitions and normalized to Talairach space), centered on the group maximum ($x, y, z = 15, -81, -3$). (*B*) Main effect of the retinotopic localizer. Increased signal ventrally in the right medial occipital cortex in response to stimulation in the upper left visual quadrant versus the other three quadrants. Brain sections of the mean T1 structural for the group are centered at the learned > new peak, showing the overlap of learning effect and localizer result. (*C*) Parameter estimates of the regressors of interest included in the SPM design matrix (i.e., learned and new conditions), extracted from each individual peak in each single-subject analyses (mean location across participants $x, y, z = 14.8, -79.7, -3.9$, SD = 3.6, 3.6, 2.1). (*D*) Group-averaged peristimulus time responses of the right occipital peak, for the learned and new conditions, demonstrating enhanced response for trained eye as compared with untrained eye. (*E*) Four representative individual SPM maps (learned > new constrast) showing the peak location of activated visual cortex in inferior calcarine region. Results are superimposed on each individual structural T1-weighted MRI (coregistered to the functional acquisitions and normalized to Talairach space).

The fact that increased visual activity in the learned condition was restricted to a single well defined cluster of voxels in medial occipital cortex suggests that the effects of learning were essentially local. No significant effect was observed in other brain areas involved in visual skill learning and attentional control (11, 26, 27). On the other hand, behavioral evidence has suggested that efficient learning in TDT might depend on attention-driven feedback influences from other brain areas (3). We therefore tested whether the increased responses in visual cortex for stimuli presented to the trained eye might be partly related to concomitant changes in the activity of distant brain areas. We performed an analysis of functional connectivity (psychophysiological interaction, see *Methods*) to identify brain regions whose activity showed a differential pattern of covariation with activation in the right occipital cortex as a function of the experimental condition (i.e., greater coupling specifically during the stimulation of either the trained or untrained eye). This analysis revealed five regions showing greater functional coupling ($P < 0.001$) with the right medial occipital cortex during the new untrained condition compared with the learned condition, including left frontal cortex, left posterior intraparietal sulcus, right inferior parietal lobul, and left and right amydalae (Fig. 3). By contrast, we found no voxel exhibiting significant increases in functional coupling with right occipital cortex during the learned condition.

Discussion

The present study provides direct evidence linking durable learning in a TDT and enhanced neural activation in early, retinotopically specific regions of the human visual cortex. We find an increased response in calcarine cortex to target-texture stimuli presented to the trained eye, relative to stimuli presented at the same retinal regions in the untrained eye and projecting to adjacent ocular dominance columns in primary visual cortex. This selective activation pattern shows that plasticity in the adult brain can be induced at the first stage of visual cortical processing, where monocular inputs are still segregated. Furthermore, such an enhancement of visual responses was observed 24 h after subjects had trained on the task for a single session, indicating a neural reorganization that could develop and persist over relatively long time delays after active stimulation (14). We found no significant increases for the learned versus new condition in other brain regions. Moreover, the effect of learning observed in early visual cortex during the learned condition

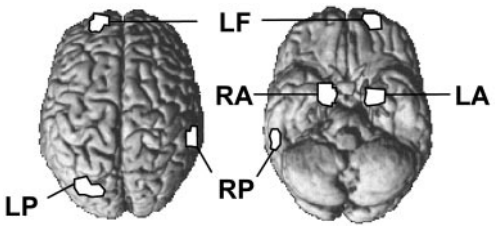

Fig. 3. Regions showing a significant coupling with activity in right medial occipital cortex specific to the new untrained condition. Significant changes in functional connectivity were observed in the left anterior middle frontal gyrus (LF, 31 voxels; *x*, *y*, *z* = −18, 63, 9; *Z* value = 4.69), bilateral amygdalae (LA, left: 26 voxels; *x*, *y*, *z* = 18, 3, −21; *Z* value = 4.41; RA, right: 19 voxels; *x*, *y*, *z* = −21, −3, −18; *Z* value = 3.99), left posterior intraparietal sulcus (LP, 37 voxels; *x*, *y*, *z* = −33, −81, 39; *Z* value = 4.35), and right inferior parietal lobule (RP; 26 voxels; *x*, *y*, *z* = 63, −36, 33; *Z* value = 4.26).

appeared to predominantly reflect local changes, independent of influences from other brain areas that covaried with visual cortical activity during the untrained condition only.

It is unlikely that the increased activation for the learned condition in our study was due to attentional effects. First, attention was controlled by a dual task performance, involving a central letter identification, which engaged attentional resources to a similar degree during the learned and new conditions. There was no evidence of ceiling or major change in performance in this central task between the different conditions. Second, although attentional effects have been reported in several retinotopic areas, including V1 (8, 28), such an explanation would imply that attentional modulation can occur selectively for the trained versus untrained eye. In the absence of previous reports of such effects, it is reasonable to conclude that increased neural activity in occipital cortex resulted from some form of local plasticity. Finally, higher level areas known to be implicated in attentional control showed no significant activation due to learning.

Learning-Related Increases in Early Sensory Cortex. Our results clearly demonstrate increased neural responses in early visual cortex and with a retinotopic (quadrant-specific) distribution, after a single training session, in humans. Learning-dependent enhanced activity has been found in early auditory and somatosensory cortical areas using MEG in trained musicians (29, 30). Using positron-emission tomography, Molchan *et al.* (31) found learning-related enhancement of activity in primary auditory cortex in a simple associative learning paradigm. Seitz and Roland (32) observed significant mean regional cerebral blood flow increases in the left sensory hand area after right-hand finger movement sequence learning. In the visual domain, only one preliminary report from Karni *et al.* (16) described a spatial extension of visual cortical activity after 4 weeks of monocular training on a TDT. Unlike Karni *et al.* (16), we acquired whole-brain images and used statistical parametric mapping to test for the learning effects across the whole brain without relying on *a priori* regions of interest. Our study provides fMRI evidence for a distinction between brain areas involved during initial exposure to the task and those showing retinotopic changes in early visual cortex after learning has occurred.

Neural Mechanisms of Plasticity. These results have important implications for understanding the possible neural mechanisms underlying TDT learning. Different hypotheses may be put forward based on previous neurophysiological work in animals.

One potential mechanism is the sharpening of V1 cell sensitivity to relevant features of the trained stimulus (5). This would allow learning to be expressed by decreasing the size of the ensemble of neurons recruited by task performance and might lead to a reduction in regional neuronal activity associated with learning (33). Similar mechanisms have been proposed for perceptual learning at a higher level of processing, such as repetition priming effects (34), involving a selective reduction of activity in areas engaged in processing specific categories of stimuli (e.g., words, three-dimensional visual objects), independent of perceptual modality (35), or retinal image size of the repeated stimuli (36). Note that these studies failed to show any learning-related decreases in early retinotopic visual areas. By contrast, our results did not reveal a regional decrease but a significant increase of activity in retinotopic visual cortex for stimuli presented in the same quadrant to the trained eye compared with the untrained eye. It is thus unlikely that lasting improvement in TDT was mediated by a sharpening of visual cell sensitivity leading to reduced assemblies of activated neurons, unless such sharpening might result from a stronger involvement of inhibitory activity mediated by lateral interconnections, which could in turn lead to an increase in the summed local neural activity. However, it is still debated whether such inhibitory activity would result in increased BOLD responses.

An alternative mechanism to account for our results might imply the enlargement of the overall size of a cortical area responsive to the trained stimulus. For example, an improvement in tasks that rely on topographical sensory representations (e.g., somatotopic localization) has been found to be associated with such cortical enlargement (37). Recent neurophysiological evidence in monkeys indicates, however, that in the visual domain there is no expansion of areas representing a trained orientation or location of visual space (6) and no increase in the proportion of cells preferring the trained orientation or location (5).

A third possible mechanism assumes contextual effects based on local reciprocal interactions. Learning-dependent increases in the responsiveness of V1 cells to the precise configuration of a trained stimulus may result from changing the influences exerted by stimuli outside the classical receptive field (1). Such contextual effects are mediated by long-range horizontal and interlaminar connections that link cells with similar orientation preference across ocular dominance columns (7, 38). Learning effects in TDT might potentially depend on similar contextual tuning mechanisms, whereby a network of horizontal connections is reinforced and integrates information coming from both the target-texture elements and the background elements (39, 40). In the present study, contextual tuning would support enhanced visual segregation of contiguous iso-oriented target lines (diagonal) from a homogeneous background of iso-oriented lines (horizontal) (Fig. 1*A*). After learning, the recruitment of larger assemblies of interconnected neurons could then produce a higher total neural response to the target texture, associated to a proportional increase in regionally specific BOLD contrast (41). Such changes in long-range horizontal connections may not develop during simple contrast or orientation discrimination tasks (compare with ''context-enabled learning'' in ref. 40), explaining why Schiltz *et al.* (33) did not find an increase in regional cerebral blood flow but a decrease when subjects trained on an orientation discrimination task over several days. We propose that contextual tuning mechanisms might constitute a plausible physiological account for the present neuroimaging data in humans.

Site of Plasticity. Our results provide strong support for the hypothesis based on previous behavioral studies (3) that monocular- and retinotopic-specific improvements in TDT can arise from changes in low-level visual pathways. In our study, performing the task with the trained eye evoked greater activity in early retinotopic cortex, but it was not associated with an increased engagement of other brain areas, remote from early visual cortex. In addition, analysis of functional connectivity

showed that the responses in visual cortex were more coupled with activity in distant but interconnected brain areas when the task was untrained, but not after the task was learned. These findings are consistent with the idea that TDT learning induced mainly local changes within early visual cortex, rather than an increased recruitment of a distributed neural network.

By contrast, performance in the new condition (untrained eye) was associated with a greater functional coupling between early visual cortex and distant areas in the parietal and frontal cortex, as well as the amygdalae. Such coupling with frontal and parietal regions may represent a greater engagement of mechanisms of spatial attention, enhancing selective processing in visual cortex specifically during the new, untrained condition (26, 42), although without producing a net increase in overall level of activity in the functionally coupled retinotopic cortex. This finding is consistent with behavioral data suggesting the need for active attentive processing during task performance to establish a subsequent lasting improvement (3, 10). Furthermore, increased functional connectivity between the amygdalae and the visual cortex in the new condition may enhance the processing of relevant visual configurations (43) and learning based on motivational signals (44), and might play a critical role in consolidation processes taking place after training (14, 15, 17, 45). This pattern of results suggests that neural changes occurring in early visual cortex after intensive practice with the task could permit a more efficient performance, despite a reduction of influences from higher-order brain areas.

In sum, we have demonstrated a functional reorganization in the early visual cortex of adult humans, observed 24 h after a single training session on visual texture discrimination. Learning produced increased neural responses in corresponding retinotopic areas only for targets presented to the previously trained eye, compared with targets presented at the same retinal quadrant to the untrained eye. These findings suggest that plastic changes occurred at the earliest stage of cortical processing where both the retinotopic and monocular organization of the visual inputs are still retained.

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